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MATCHING MORPHOLOGY AND DIET IN THE DISC-WINGED BAT *THYROPTERA TRICOLOR* (CHIROPTERA)

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The dietary niche and morphological adaptations of a species should be highly correlated. However, conflicting selective pressures may make predictions about diet difficult without additional knowledge of a species' life history. We tested the reliability of predicting a bat's diet from its wing morphology using data for Spix's disk-winged bat (*Thyroptera tricolor*). The species had been predicted to fall within either the aerial hawking or gleaning foraging group. We compared the results of a theoretical (canonical discriminant function analysis of morphology) and an applied (analysis of droppings) method of diet determination. Our results place *T. tricolor* in the gleaning functional group with a 77% probability according to morphology. Correspondingly, a large proportion of the diverse diet consisted of nonflying prey, such as spiders, insect larvae, and other silent prey, which should be difficult to detect using echolocation. Although some flying prey were taken, it is clear that *T. tricolor* regularly gleans prey from surfaces, indicating that for this species, morphology is a useful indicator of diet. However, the breadth of the diet; the high proportion of jumping spiders, leafhoppers, and insect larvae; and the extremely small size of prey were unique features of the diet that could not be predicted from morphology alone. Thus, although comparative statistical methods and the analysis of wing morphology may be helpful to predict the general ecological niche, only detailed investigation of the life history may yield the detail needed for understanding the link between morphology and ecology of individual species.

Key words: discriminant function analysis, ecological niche, fecal analysis, gleaning, wing morphology

Many morphological and life-history traits contribute to the adaptations of species to their ecological niche. The more specific such adaptations are, the greater the constraints, and the increasingly narrow the niche becomes. At the same time, specialization may reduce competition or even allow exploitation of an otherwise unused resource. For example, depending on their flight morphology and echolocation call structure, insectivorous bats can only detect and catch some of the theoretically available arthropods. Thus, the sensory and morphological adaptations of bats can directly influence the prey types actually available, and knowledge of foraging strategy or diet can reveal the degree of a species' flexibility, prey selection, or both and thus provide valuable information about their ecology.

Bats, especially insectivorous species, can be classified into functional groups according to their foraging strategy and food (Findley 1993; Kalko 1998). Foraging strategy in turn often can be predicted based on morphological traits such as wing and ear shape (Fenton and Bogdanowicz 2002; Norberg and Rayner 1987). For example, large ears characterize bats that rely on prey-generated sounds. Such bats typically glean prey from surfaces. This passive listening strategy often is connected to foraging in the understory, which requires species to have broad, large wings allowing high maneuverability. In contrast, species that detect and localize prey using echolocation in open space have small external ears and long, narrow wings, the latter being a prerequisite for fast flight (Norberg and Rayner 1987). Finally, species with an intermediate morphology often are adapted to foraging along the edge of vegetation and in forest gaps, an environment of intermediate complexity. These adaptations to different flight modes and foraging strategies may be reflected in the size of the brain and its component parts (Ratcliffe et al. 2006; Safi and Dechmann 2005; Safi et al. 2005) as well as the structure of echolocation calls (Schnitzler and Kalko 2001).

In reality, few bat species are restricted to one of the hunting strategies described above. Instead they are able to use mixed strategies, or other factors may influence their phenotype (e.g., Ratcliffe and Dawson 2003). For example, seasonal long-distance migration may necessitate a compromise in flight

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morphology. Consequently, it can be difficult to classify species according to morphology, especially if their ecology is unknown. One such example is Spix's disc-winged bat (*Thyroptera tricolor* (Spix)), a small (3.0- to 4.5-g) insectivorous bat found from southern Mexico to central Brazil in the Neotropics. The morphology of *T. tricolor* has been used to generate conflicting predictions concerning foraging strategy. It has small ears and rather long and narrow wings, typical for aerial insectivores. However, low wing loading led Norberg and Rainer (1987) to predict slow, maneuverable flight similar to that of gleaning species. Similarly, parameters of the echolocation call of *T. tricolor* and closely related *T. discifera* (Fenton et al. 1999; Tschapka et al. 2000) led to contradicting conclusions. The low intensity and thus short detection range resembled that of a gleaning bat, whereas unmodulated frequencies and relatively long call duration seemed more indicative of edge- and gap-foraging specialists, which normally call at higher frequencies with a broader bandwidth than *T. tricolor*. Although some authors expected this species to be a foliage gleaner (Findley and Wilson 1974), it has also been predicted to employ an aerial insect-eating strategy (Kalko et al. 1996; LaVal and Fitch 1977; Reid 1997; Wilson 1973).

Little is known about the status and ecology of this lowland rain forest species, whose most peculiar characteristic is the morphological adaptation to its unusual roosting behavior; *T. tricolor* has well-muscled, moistened suction-disks on the base of its thumbs and at the ankles (Wilson and Findley 1977). With the help of these suction disks it clings to the smooth surface of young, rolled leaves of *Heliconia* and other musoid plants in stable mixed-sex groups of up to 11 individuals (Vonhof and Fenton 2004; Vonhof et al. 2004).

Our aim was to determine the foraging strategy of *T. tricolor* using 2 methods. First, we used a canonical discriminant function analysis to predict the functional group *T. tricolor* belongs to from various wing morphology traits. This allowed us to predict which of 3 main functional groups (dense habitat gleaners, edge and gap foragers, or open aerial insectivores) *T. tricolor* should be placed in according to its morphology. Second, we assessed prey selection by analyzing droppings to see if the theoretical prediction was matched by the diet. For this purpose, feces were collected from roost leaves. Because *T. tricolor* does not occur in areas with an extended dry season (Reid 1997), we evaluated the potential influence of the short dry season and reproductive period on prey selection. We paid special attention to the ecology of prey species, to infer knowledge about the bats habitat requirements and hunting strategy.

Materials and Methods

Assignment of functional group.—First, we used a multivariate analysis of variance (MANOVA) to test whether morphological traits differed between foraging strategies (functional group or guild; classifications from Kalko et al. [1996]). We then used a canonical discriminant function analysis to reduce the number of morphological variables and at the same time to predict the foraging strategy of *T. tricolor* based on the canonical variables (data for all species taken from Norberg and Rayner [1987]). Canonical discriminant function analysis is a dimension-reduction technique related to principal component analysis and canonical correlation. The canonical variables represent linear combinations of the quantitative variables, which summarize between-class variation in much the same way that principal components summarize total variation (SAS Institute Inc. 1993). To place these analyses in context, we analyzed data for body mass, wingspan, wing area, aspect ratio, and wing loading of *T. tricolor* and 44 other species. For a subset of 33 species, wing tip measures (tip length, tip area, and tip index) also were available. Therefore, we performed all analyses twice; once with the larger data set using fewer morphological measures and a 2nd time with more variables relevant to flight performance, but with fewer species. We only used data for species from the 3 major functional groups (open aerial insectivores, edge and gap foragers, and gleaning species). We used natural logs to convert all data, except for functional group, before analyses. In a preliminary test, body mass was correlated with all wing variables ($0.06 \geq P > 0.0001$). As a result, we calculated the least squares residuals as a function of body mass after a double logarithmic conversion of the morphological variables. The resulting relative flight morphological variables were unrelated to body mass and we used them for all subsequent analyses.

Study site and period for collection of fecal samples.—The field site comprised a total of about 7 ha in the immediate vicinity of the Caño Palma biological field station (10°37′N, 83°32′W), operated by the Canadian Organization for Tropical Education and Rainforest Conservation in the Barra del Colorado Wildlife Refuge, Costa Rica. We collected fecal pellets from February to May 1998. The vegetation consists of alluvial, tropical lowland rain forest and seasonally inundated palm rain forest (Gomez 1986). The climate is classified as ''very humid, very hot, without a distinct dry season (except fewer than ten days in March)'' (Herrera 1986:118). Average yearly rainfall is about 5,000 mm.

Sample collection.—Roosts were found by searching the study area systematically for all suitable leaves every 3–7 days. Roosting bats were captured in the course of another ongoing study (Vonhof and Fenton 2004; Vonhof et al. 2004). For the removal of fecal samples, roost leaves had to be destroyed, but they were not limited in the study area, and bats never reused leaves after capture anyway (Vonhof et al. 2004). We only collected fecal samples from roosts still occupied by bats, because we found decomposers (larvae of sarcophagid flies—Pape et al. 2002) in the feces almost immediately after bats occupied a new roost-leaf. Feces in leaves deserted by the bats would have been exposed to destruction by the fly larvae for longer periods, rendering identification, especially of softer remains, more difficult. We collected a maximum of 10 pellets from each roost leaf; these were frozen at −20°C for several hours to kill fly larvae, and then dried for storage. All procedures meet guidelines recommended by the American Society of Mammalogists (Animal Care and Use Committee 1998). All of the research also was carried out in concordance with Costa Rican laws.

Analysis of samples.—We analyzed a total of 150 pellets from 30 different roosts (5 pellets each). Pellets were viewed with a binocular microscope after soaking them in water for half an hour and then teasing them apart with dissecting needles and pointed tweezers. Remains of arthropods were classified to order and in some cases to family.

We quantified prey categories by frequency (presence or absence of a taxon) rather than volume percentage (percentages obtained from frequency of occurrence—McAney et al. 1991) as in Beck (1995), because each fecal pellet contained a large proportion of unidentifiable matter. This method avoided overestimation of strongly sclerotized taxa, which are more resistant to digestion or remain in the digestive tract longer than softer ones (Rabinowitz and Tuttle 1982). For the

same reason, Lepidoptera and Coleoptera only were included when their remains made up more than one-third of a pellet. In contrast, soft-bodied Neuroptera and Isoptera were counted as present even if only a single fragment could be found. It was impossible to assign isolated pieces of thorax or abdomen to a taxon because each pellet contained fragments of 5–8 orders. Statistical analyses, except for the determination of prey preferences (see below), were performed with SAS 8.1. (SAS Institute Inc. 1993)

Size measurements.—We measured fragments of arthropods from the feces on a millimeter grid (graph paper) under a dissecting microscope to estimate the size of prey organisms. This allowed us to compare them with intact specimens from the insect collection of the Instituto Nacional de Biodiversidad (Costa Rica) and specimens collected at Caño Palma. We defined 3 size groups after Beck (1995): small (arthropods with wingspan or body length of 2–5 mm), medium (5–20 mm), and large ($\geq$20 mm).

Preference of prey taxa.—We calculated frequency of occurrence (proportion of each prey taxon) of all prey taxa for each group of bats and each collection date following the method of Safi and Kerth (2004). Using the compositional analysis method outlined in Aebischer et al. (1993) after Aitchinson (1982), we assessed the bats' preferences for prey taxa, assuming equal availability of all taxa because abundance of the prey groups was unknown.

Influence of climate and reproductive state on diet.—The first 3 months (February, March, and April) of the study were unusually dry as a consequence of El Niño, and frequently several days passed without rain. In March and May there were periods of heavy precipitation causing the entire study area to be flooded up to depth of 0.5 m. We hypothesized that these climatic conditions would influence the development of certain insects, thereby influencing prey selection of *T. tricolor* if they were opportunistic feeders. We obtained daily measurements of the amount of rainfall (in mm), as well as maximum and minimum temperature (in °C) from a weather station at Caño Palma. In our analysis, we calculated the mean of each of these parameters from the 5 days before we collected fecal pellets.

The beginning of the rainy season coincided with the birth of the 1st young, pregnancy having been discernible in the females beginning in mid-March. Pregnancy and lactation both result in increased energy demand for bats (Racey and Speakman 1987) and we predicted that there would be a change in diet over the course of the reproductive period. Thus, we divided the diet data into 2-week collection periods, to detect a change in the composition over time.

We then tested whether each of the variables described above influenced the frequency of prey taxa in the diet of *T. tricolor*. Because the frequency data were not normally distributed, we used non-parametric tests (Kruskal–Wallis) with prey taxon as the dependent variable ($n = 10$) and maximum temperature, minimum temperature, rainfall, and collection period as independent variables to assess overall changes in the relative frequency of prey types in response to each factor. During 1 collection period only 3 samples were obtained and we excluded that period when testing for the influence of collecting period. Frequencies of prey groups were not correlated with one another and it was not necessary to reduce the number of dependent variables using principal component analysis.

Results

Assignment of functional group.—Morphological traits differed between functional groups (MANOVA large data set: Wilk's lambda = 0.4, $F = 5.5$, $d.f. = 8, 76$; $P < 0.0001$; MANOVA small data set: Wilk's lambda = 0.2, $F = 3.5$, $d.f. = 14, 48$; $P = 0.0006$). The canonical discriminant function analysis produced 2 canonical variables for each data set. Resubstitution of the original data set, using the 2 canonical variables, allowed us to correctly classify 73% of the species to the original functional group in each data set. Using the canonical discriminant function analysis based on the complete set of 44 species and the subset of 33 species for which we had wing tip measurements, *T. tricolor* was assigned to the gleaning functional group with 77% certainty in both cases (large data set: probability of 1st assigned functional group, 77% [gleaner], 2nd functional group, 22% [edge and gap]; small data set: 1st functional group, 77% [gleaner], 2nd functional group, 23% [edge and gap]; results for complete data set are available from authors). The scores of *T. tricolor* for the canonical variables lie within the 95% confidence ellipse of the gleaners but were close to the edge and gap-foraging bats (where several authors have classified the species). There is no overlap in morphology between *T. tricolor* and values for open aerial insectivores (Fig. 1).

General diet.—*Thyroptera tricolor* ate a wide variety of prey consisting of 9 orders from 2 classes of arthropods (with a total of 10 prey categories, because larvae were counted separately; Fig. 2). We identified jumping spiders (Aranea), which were taken most frequently (frequency = 0.93), by the shape of the tarsi. In order of importance, Aranea were followed by leafhoppers (Homoptera) from the suborder of Fulguroidea (frequency = 0.81), Lepidoptera (frequency = 0.63), and Diptera (frequency = 0.59) from both suborders (Nematocera and Brachycera). The next most frequent prey group was larvae (frequency = 0.43), although we could not distinguish between the larvae of Hymenoptera and Lepidoptera. Less frequent, but still regularly taken over the entire sampling period, were beetles (Coleoptera, frequency = 0.29). We could occasionally identify members of the family Curculionidae, but identification of other groups was not possible. Earwigs (Dermaptera, frequency = 0.28) were observed at a similar frequency, followed by adult Hymenoptera (frequency = 0.25), lacewings (Neuroptera, frequency = 0.23), and termites (Isoptera, frequency = 0.1). The latter were found only in 2 cases. Each pellet contained remains of up to 8 orders, sometimes several different species in the same order, particularly in the case of spiders. Many of the prey taxa were nonvolant (larvae, spiders, and many Curculionidae), infrequently volant (Homoptera), diurnal (most flies), or were likely taken while resting. The latter was evident from the bite patterns on wing fragments of Coleoptera, Dermaptera, and Homoptera, which remained folded in the feces.

Prey size.—The estimate of size reconstructed from comparisons between fragments and whole specimens indicated that most prey consumed were small, with a wingspan or body size of 2–5 mm or less. Single fragments indicated that medium-sized prey (up to 16 mm) were occasionally taken. This category may be underrepresented because of the habit of many bats of culling indigestible body parts of insects such as legs or wings before consuming the rest.

Prey preferences.—Our composition analysis (Table 1) indicated a clear preference for Aranea and Homoptera over all other prey taxa. Both groups were observed significantly

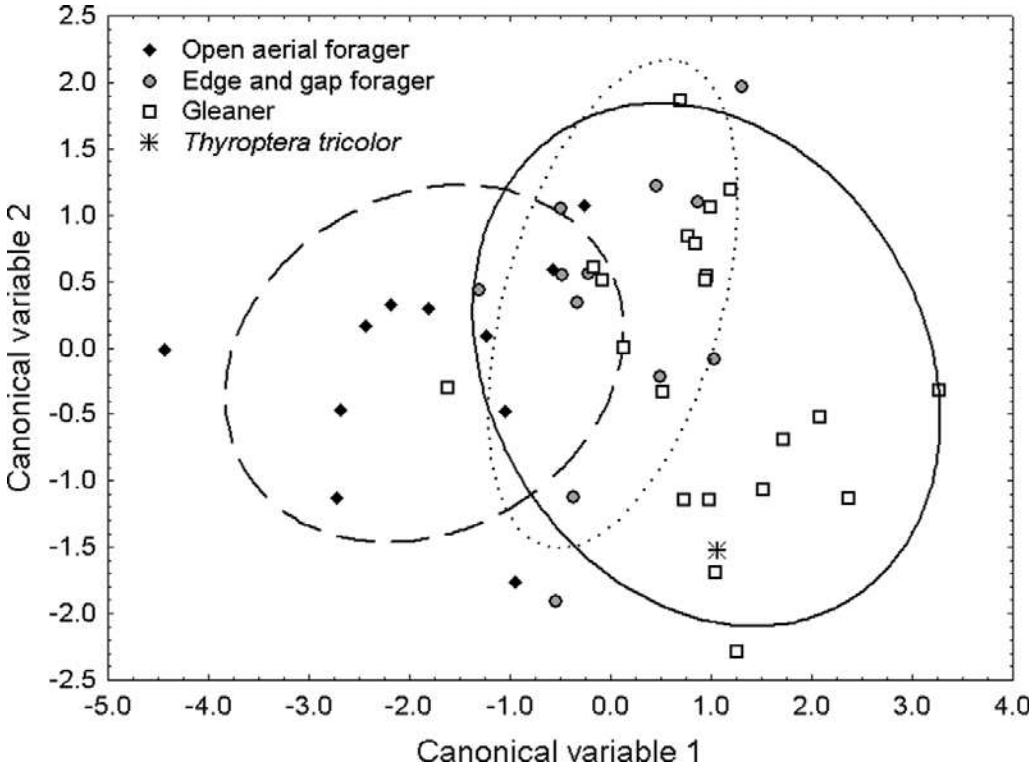

FIG. 1.—Canonical variables and 95% confidence ellipses separated into functional groups for 44 bat species; open aerial species, dashed line with filled diamonds; edge and gap species, dotted line with gray circles; gleaners, solid line with open boxes. Values for *Thyroptera tricolor* (star) lie in the 95% confidence ellipse of gleaning bats and outside the overlap area with the edge and gap bats.

more often in fecal samples than were any other taxa consumed. In addition, prey occurring at intermediate frequencies (Diptera, Lepidoptera, and larvae) were consumed significantly more often than Neuroptera, Coleoptera, Hymenoptera, and Isoptera, and all taxa were preferred over Isoptera, which were only found twice.

Influence of climate and reproductive state on diet.—None of the variables we tested (minimum and maximum temperature, precipitation, and collection period) had a significant influence on the frequency of occurrence of any prey taxa. Sample size was always 30 (the number of roost-leaves we collected feces from) except in the case of collection period ($n = 4$, after exclusion of the period containing only 3 samples). For minimum temperature, P values varied from 0.20 to 0.71 (range 21.8–27.9°C, $d.f. = 20$); for maximum temperature, from 0.21 to 0.66 (range 27.1–31.8°C, $d.f. = 20$); for rainfall, from 0.11 to 0.77 (range 0–63 mm, $d.f. = 14$); and for collection period, from 0.06 to 0.93 ($d.f. = 3$). Thus, the variables were all far from significant with the exception of the influence of collection period on the prey taxon Diptera, with $P = 0.06$.

DISCUSSION

Various studies have provided evidence for a connection between morphology and foraging strategy of bats (e.g., Fenton and Bogdanowicz 2002; Fenton and Rautenbach 1986; Norberg and Rayner 1987). *T. tricolor* was expected to be mainly a cluttered-space aerial insectivore (Kalko et al. 1996) based on its small funnel-shaped ears, echolocation call structure, and well-developed tail membrane. Alternatively, this species also had been predicted to be a gleaning species, based on the average aspect ratio and low wing loading associated with highly maneuverable flight (Norberg and Rayner 1987), and low-intensity echolocation calls (Fenton et al. 1999). Our canonical discriminant function analysis of wing morphology data corrected for body mass clearly placed *T. tricolor* in the gleaning functional group. We conclude that the foraging strategy of this species is probably mixed between

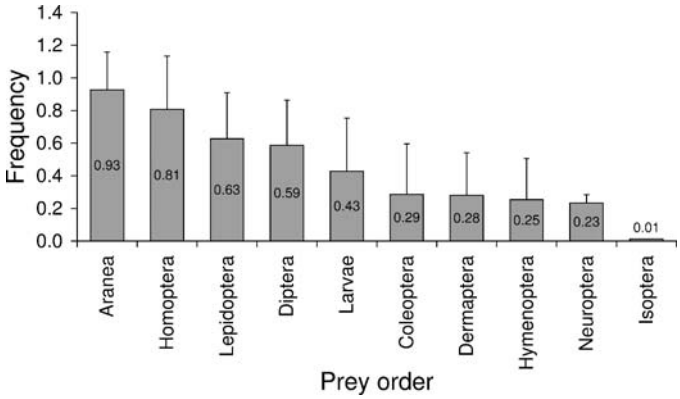

FIG. 2.—Frequencies of the 10 prey categories identified from feces of *Thyroptera tricolor* ranked according to the preference determined by compositional analysis.

TABLE 1.—Prey preferences, as assessed by pairwise comparisons between groups of prey eaten by *Thyroptera tricolor*, using *t*-tests. *P* values, above the diagonal, indicate differences in frequency of use between items; *t*-values are given below the diagonal. Asterisks indicate probability that frequencies were the same: ***: $P < 0.0001$; **: $P < 0.001$: *: $P \leq 0.05$; ns: $P > 0.05$.

	Aranea	Homoptera	Diptera	Lepidoptera	Larvae	Dermaptera	Neuroptera	Coleoptera	Hymenoptera	Isoptera
Aranea		ns	**	**	**	***	***	***	***	***
Homoptera	1.99		*	*	*	***	***	***	***	***
Diptera	2.87	−2.58		ns	ns	*	***	**	***	***
Lepidoptera	2.77	−2.34	0.47		ns	ns	**	**	**	***
Larvae	3.10	−2.59	−1.07	−0.54		ns	**	**	**	***
Dermaptera	4.23	−3.97	−2.63	−1.99	−1.99		ns	ns	ns	***
Neuroptera	5.17	−4.93	3.98	−2.80	−2.92	−1.26		ns	ns	***
Coleoptera	5.10	−4.92	−3.55	−3.23	−2.99	−1.52	−0.15		ns	***
Hymenoptera	5.13	−5.02	−4.02	−2.92	−2.96	−1.03	−0.03	0.13		***
Isoptera	18.90	−19.16	−14.60	−12.75	−11.44	−7.83	−6.15	−5.22	−6.16	

background cluttered-space aerial foraging and gleaning, leaning heavily toward gleaning, at least at our study site.

A large emphasis on gleaning was confirmed by our fecal analysis, which demonstrated that *T. tricolor* regularly eats nonflying prey. The 2 most preferred prey taxa were Aranea, particularly jumping spiders, and Homoptera, both of which are found on the surfaces of vegetation and not in midair. We also regularly recorded the remains of wingless larval Lepidoptera, Hymenoptera, or both, the remains of weevils (often incapable of flight), (diurnal) flies, and the wings of beetles and earwigs, which we found folded into resting position, all of which were consistent with gleaning as well. *T. tricolor* likely also catches some prey in flight, because most of the arthropod taxa found in the feces included some volant species. Nonetheless, most of the prey we identified cannot fly and we propose that *T. tricolor* is primarily a foliage gleaner. This is supported by observations of DKND and MJV, who saw 2 light-tagged adult males flying close to the ground, as well as beneath the canopy, always flying slowly, and often hovering around vegetation.

Examinations of previous data on the diet of *T. tricolor* have been equivocal with respect to its foraging strategy. Whitaker and Findley (1980) analyzed fecal pellets from 23 Costa Rican individuals and found evidence of Lepidoptera and Coleoptera in almost all samples. Other prey categories identified by these authors were Diptera, Hemiptera, Homoptera, and a small percentage of Araneida, which were not further identified. These authors also mention the presence of entire dipteran larvae, which are probably the same decomposers as found by Pape et al. (2002) and were not consumed by the bats. Howell and Burch (1973) examined a single *T. tricolor* whose stomach and feces contained lepidopteran remains. In addition to the prey groups reported in the literature, we found Hymenoptera, Neuroptera, Dermaptera, insect larvae, and Isoptera. Aranea, which occurred in only 13% of the pellets in the study of Whitaker and Findley (1980), were present in 93% of our samples. Insectivorous bat diets may vary considerable between sites and between seasons, and the differences between studies in the relative proportions of different prey taxa in the diet likely reflects variation in the relative abundance of these groups at different sites or possibly prey preferences due to nutrient requirements or energetic constraints.

The high frequency of jumping spiders in the diet of *T. tricolor* is unusual among bats, and ours is the 1st study to demonstrate the regular occurrence of this prey taxon in the diet of any bat species. Although *Kerivoula papuensis* has been shown to regularly feed on spiders (Schulz 2000), it mainly captures orb-weaving spiders in their webs. Other bat species occasionally eat spiders (e.g., *Antrozous pallidus*—Johnston and Fenton 2001; *Eptesicus furinalis*—Aguirre et al. 2003; *Myotis albescens*—Aguirre et al. 2003; *M. emarginatus*—Beck 1995; Krull et al. 1991; *M. mystacinus*—Beck 1995; Taake 1992; 1993; *M. nattereri*—Siemers and Schnitzler 2000), but they are not a regular component of their diet. We observed only a small number of fragments of orb-weaving spiders among the Aranea in fecal pellets, and it is likely that *T. tricolor* regularly gleans spiders from leaf surfaces rather than taking them from threads or webs. DKND has observed 1 captive *T. tricolor* eating a spider it had caught by landing on the screen wall of a flight tent. Even though the spider was small, several legs were bitten off and dropped by the bat. Culling of wings and legs makes it impossible to count numbers of individuals eaten, and at least partly explains why prey generally could not be identified beyond the level of order.

Our analysis showed that most prey was small, in contrast to what is known about most other gleaning species. For example, the similarly sized *Micronycteris microtis*, which is assigned to the same functional groups with almost the same probabilities as *T. tricolor* (gleaner: 77%; edge and gap: 26%), typically feeds on arthropods equal to or larger in size than the bats themselves (Kalka and Kalko 2006). This difference in the size of prey consumed by those 2 species of bats cannot be predicted with a theoretical method such as canonical discriminant function analysis. In fact, detection of the small prey of *T. tricolor* by echolocation should be difficult when gleaning from the surface of vegetation (providing high levels of acoustic clutter). The echolocation calls of *T. tricolor* have the intensity but not the duration or harmonic structure typical of gleaners (Fenton et al. 1999). Further analysis and observation of hunting bats under experimental conditions will be necessary to better understand their use of echolocation. The European *M. nattereri* is able to detect silent and motionless prey including spiders on or close to the vegetation by echolocation (Siemers and Schnitzler 2000). Similarly,

M. microtis detected motionless insects on the surface of leaves in a flight cage, and was able to distinguish between dummies and real animals (Locher 2000). This species as well as several species of *Myotis* also apply a mixed strategy between gleaning and aerial hawking (Kalka and Kalko 2006; Ratcliffe and Dawson 2003).

To test for opportunistic hunting in *T. tricolor*, we analyzed fecal samples collected the day after a termite nuptial flight. The only 2 fragments of termites (Isoptera) we found were in this sample. But in case of opportunistic hunting we would have expected much more after the huge numbers of these insects the night before. Other observed insect swarming events, such as those of beetles (which are a common prey item) or true bugs, also were not mirrored in the diet. This indication of nonopportunistic foraging is confirmed by the lack of change in diet over time in spite of the distinct change in climate, especially precipitation, that should have strongly influenced prey availability.

When we investigated the influence of various parameters on the diet, we found no change in consumption of the most important prey groups in connection with either collecting period or climate. However, several fragments such as the heart-shaped thorax ornament of a beetle, which was observed in several samples collected within a few days, but then was not encountered again, hint at temporary preferences at the prey species level. This is supported by the comparison of 2 groups of bats, whose feces were collected on the same day and contained the same rare fragments. Similarly, we were unable to detect any change in prey selection as a function of reproductive state, which should have been reflected by a change in diet over time.

Our study indicates that *T. tricolor* feeds on a wide variety of small arthropods, most of which it obtains by gleaning. We found that the morphology of a species is a useful predictor of foraging strategy, but more detailed studies of the diet turn up unexpected patterns of prey consumption that could not be predicted by morphology alone. The foraging strategy of *T. tricolor* needs to be investigated experimentally to understand the yet unexplained structure of the echolocation calls, which may reveal how these bats detect silent or near-silent small prey on surfaces. Furthermore, refined understanding of geographic and temporal variation in foraging style and diet will help to more completely understand the complicated relationship between ecology and morphology.

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